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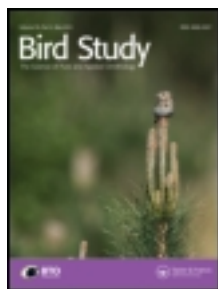
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Growth of Little Stint *Calidris minuta* chicks on the Taimyr Peninsula, Siberia

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Growth of mass and linear body dimensions (bill, tarsus and wing length) was studied in the Little Stint *Calidris minuta* at several locations on the Taimyr Peninsula, Siberia (73°–76°N) in 1983–94. Little Stints fledged at near-adult body mass, at 15 days of age. Growth followed an S-shaped pattern which was best described mathematically by a logistic curve. Curves of this type showed that growth was similar between study sites and years, although there were differences in mass development during the first days after hatching, perhaps related to weather conditions. When the logistic growth curve was used, K_L (the standard measure of maximum growth rate) was 0.285. Conversion of this parameter to another S-shaped curve, the Gompertz curve which has been widely used to describe wader chick growth, yields $K_G = 0.194$. This is higher than predicted from an allometric relationship based on 15 other precocial wader species, and might be related to the Little Stint's high latitude breeding range.

In a review of published growth rates in precocial shorebirds (Charadrii), Beintema & Visser¹ listed data for 15 species. A minority of these concerned arctic-breeding species, despite the fact that many shorebirds (especially in the family Scolopacidae) breed in arctic or subarctic regions, and that shorebirds make up a large proportion of arctic bird communities. This is understandable given the

difficulty of collecting data on highly mobile precocial chicks such as waders in general, and in remote arctic areas in particular. Considering that arctic birds can only reproduce successfully when they are able to complete breeding activities within the short time frame set by the climate,² and that selection for rapid growth might therefore be expected, additional data on growth in arctic waders are of interest.

This paper describes hatchling dimensions and growth of chicks up to fledging age in the Little Stint *Calidris minuta*. There are no

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previous published growth data for this species, which is among the smallest existing precocial birds. Despite its small size, the Little Stint has a quite northerly breeding distribution, with highest densities in the typical and arctic tundra subzones between 72°N and 75°N in Siberia.^{3,4}

Shorebird chicks, including Little Stints, often fail to grow heavier and may lose mass during the first day(s) after hatching. Because our data were collected in a variety of years and areas, we were able to test whether hatchling body reserves were always lost during the first few days of life or whether chicks sometimes hatched in conditions where growth could commence right away.

METHODS

Growth of Little Stints was studied at several locations scattered over the northern half of the Taimyr Peninsula in north-central Siberia, Russia, in a number of years between 1983 and 1994 (Fig. 1 & Table 1). Data were collected by different researchers, but general methods were similar in all studies. Nests were located during

laying or incubation. Chicks were ringed, weighed and measured while still in the nest, or whenever broods were encountered in the tundra. Not all observers took the same measurements on chicks, so the number of data points differs depending on the biometric concerned. However, methods used in taking measurements were the same for all observers. Body mass (to nearest 0.1 or 0.5 g) was measured on the majority of chicks, using a spring or beam balance. Bill length (exposed culmen) was also measured in most cases, whereas tarsus and wing length (maximum chord) were recorded less often. Wing length was measured only after the primary feathers had appeared beyond the down, except for seven hatchlings at Cape Sterlegov in 1994.

For describing growth, only chicks were used of which the age was known with an accuracy of ± 24 h. This condition was met for chicks which were ringed when still in the nest, as we found that the great majority of broods leave the nest well within 24 h after hatching. Some additional data were used from chicks which had been first ringed when already out of the nest, but of which the hatching date was

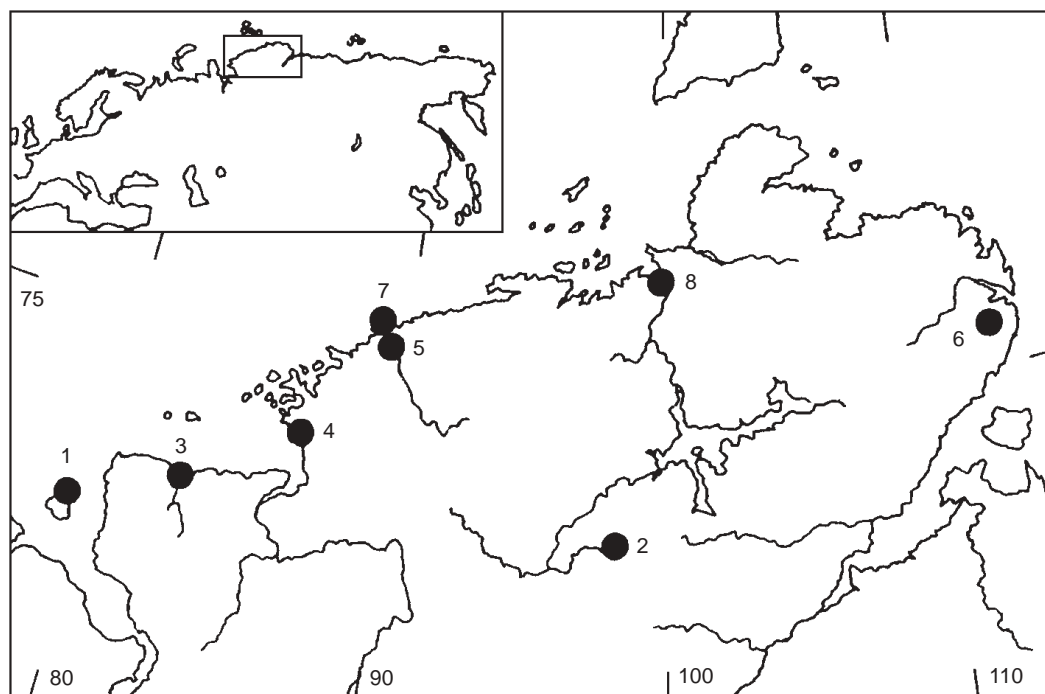


Figure 1. Map of the Taimyr Peninsula showing study area locations (numbers refer to Table 1).

Table 1. Study areas and years, and number of Little Stint chicks of four age classes measured.

No.	Site	Coordinates		Year	N ₀	N ₁₋₅	N ₆₋₁₀	N _{>10}	Obs
1	Sibiriakov Island	72°44'N	79°08'E	1990	1	0	0	2	PC
2	Malaya Logata River mouth	73°25'N	98°25'E	1989	47	26	2	0	WK
3	Uboinaya River	73°37'N	82°20'E	1984	7	8	0	0	PT
4a	Pyasina River mouth	74°08'N	86°45'E	1990	28	67	11	3	GN,HH
4b	Pyasina River mouth	74°08'N	86°45'E	1991	1	3	0	0	WK,PC
5	Lenivaya River	75°16'N	89°30'E	1983	23	5	1	0	PT
6	Pronchishchev Lake	75°16'N	112°28'E	1991	25	14	5	6	HS,MR
7	Sterlegov Cape	75°25'N	89°08'E	1994	7	0	0	0	HS
8a	Knipovich Bay	76°05'N	98°32'E	1990	74	66	12	3	PT,MS
8b	Knipovich Bay	76°05'N	98°32'E	1991	82	35	0	0	PT,MS
Total					295	224	31	14	

Obs, initials of contributing authors.

known from a recent visit.

Growth curves were fitted to the data with the versatile growth model of Schnute.^{5,a} Additionally, three classical growth curves (logistic, Gompertz and Von Bertalanffy) were fitted. These are special cases (submodels) of the Schnute model; their descriptive power was compared to the general model using *F*-tests on the residual sums of squares. Because of lack of independence between multiple data points obtained from individual chicks, approximate standard errors for the parameter estimates were derived using the jackknife technique.^b In addition, parameter estimates for three subsets of the data which included chicks from all age classes up to fledging were used to obtain a measure of the inter-dataset variability of body mass growth.

To avoid problems with mass loss during the first day(s) after hatching,^c the body mass growth curve was fitted to data for chicks of one day and older only. All data were used in fitting the curves for linear body measure-

ments, as these increased from the first day onwards.

RESULTS

Mean biometrics of hatchling Little Stint chicks, measured when still in the nest, and of chicks measured around fledging are given and compared with adult size in Table 2. Fledging (i.e. becoming able to fly at least several tens of metres) occurs at about 15 days in Little Stints; it may be retarded a few days when conditions for growth are unfavourable.

Body mass did not increase from the first day onwards, but remained stable for about one day before growth started. Mean body mass of one-day-old chicks (4.25 g, *se* = 0.04, *n* = 73) was not significantly different from that of hatchlings (Student's *t*-test, *t*₁₁₅ = 0.35, *P* = 0.73). However, the data collected in different years and at different localities were not consistent in this respect: in a two-way analysis of variance with age (0 or 1 day) and data set as factors,

Table 2. Biometrics of neonate and fledgling (15 days or older) Little Stints in Taimyr. Adult biometrics^d are given for comparison.

	Neonate size			Fledgling size			Adult size
	Mean	se	n	Mean	se	n	
Body mass (g)	4.27	0.02	177	23.84	2.91	8	26.7
Bill length (mm)	7.32	0.03	222	15.68	0.21	8	18.2
Tarsus length (mm)	18.12	0.16	29	21.70	0.47	8	21.9
Wing length (mm)	12.00	0.31	7	71.60	0.44	5	99.6

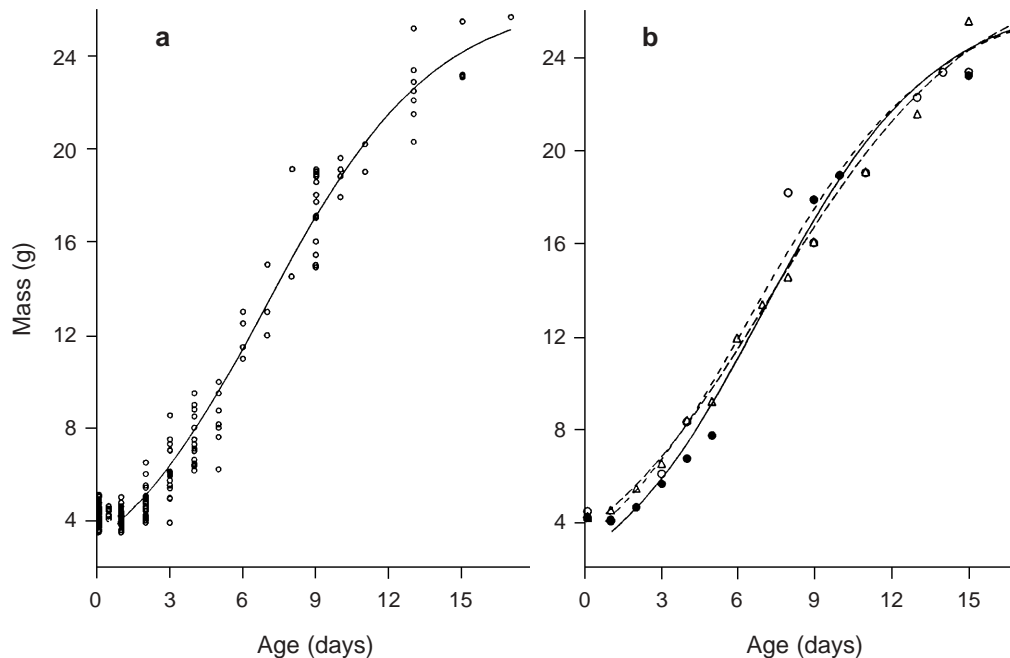


Figure 2. Growth of body mass in Little Stints on the Taimyr Peninsula. (a) Observations and the fitted logistic curve for all years and locations combined; (b) means and fitted curves for Knipovich Bay 1990 (●—●), Pronchishchev Lake 1991 (○---○) and Pyasina Delta 1990 (Δ---Δ).

both the effect of data set ($F_{5,249} = 4.16$, $P = 0.001$) and its interaction with age ($F_{5,249} = 4.34$, $P < 0.001$) proved significant, whereas the main effect of age was not ($F_{1,214} = 0.08$, $P = 0.77$). Whereas at Pronchishchev Lake in 1991 mean body mass of chicks decreased by 0.36 g over the first day after hatching ($t_{26} = 2.48$, $P = 0.02$), the mean for chicks at the Pyasina delta in 1990 increased by 0.26 g over the same interval ($t_{49} = -2.57$, $P = 0.013$), while the other data sets showed no significant change. On the second day and later, mass increased in all data sets (mean at age 2 = 4.87 g, $se = 0.13$, $n = 38$, age 2 versus 1, $t_{46} = -4.60$, $P < 0.001$), most rapidly again at the Pyasina River mouth in 1990. Thus in the Pyasina mouth in 1990, growth started more rapidly than in the other studies. This was however not reflected in higher masses of chicks older than one week.

Data of chicks of one day and older were used to fit the body mass growth curve (Fig. 2a). The logistic submodel fitted the data as well as the four-parameter model (comparing residual sums of squares, $F_{1,210} = 3.35$, $P > 0.05$), while Gompertz ($F_{1,210} = 29.5$, $P < 0.01$) and Von

Bertalanffy's ($F_{1,210} = 46.0$, $P < 0.01$) equations explained significantly less of the variance than the four-parameter model. There were three data sets with sufficient observations to fit set-specific mass growth curves: Knipovich Bay 1990, Pronchishchev Lake 1991 and Pyasina Mouth 1990. Except for a slower early growth at Knipovich Bay, the fitted curves are quite similar (Fig. 2b). The means ($\pm se$) for the logistic parameter estimates of these three curves were: 0.281 ± 0.021 for K_L , 26.82 ± 1.16 for A , and 7.03 ± 0.44 for T .

The fit of a logistic curve was as good as that of the general Schnute model for tarsus ($F_{1,58} = 0.43$, $P > 0.05$) and wing length ($F_{1,14} = 0.01$, $P > 0.05$). Although the fit of the logistic and the Schnute model differed significantly for bill length ($F_{1,431} = 6.41$, $P < 0.01$), the difference in proportion of variance explained was very small (0.1%) and logistic curves are presented for all variables (Table 3, Fig. 3). Although no formal test was possible, logistic equations seemed to fit the data as well as or slightly better than Gompertz or Von Bertalanffy's curves for all structures, and produced more

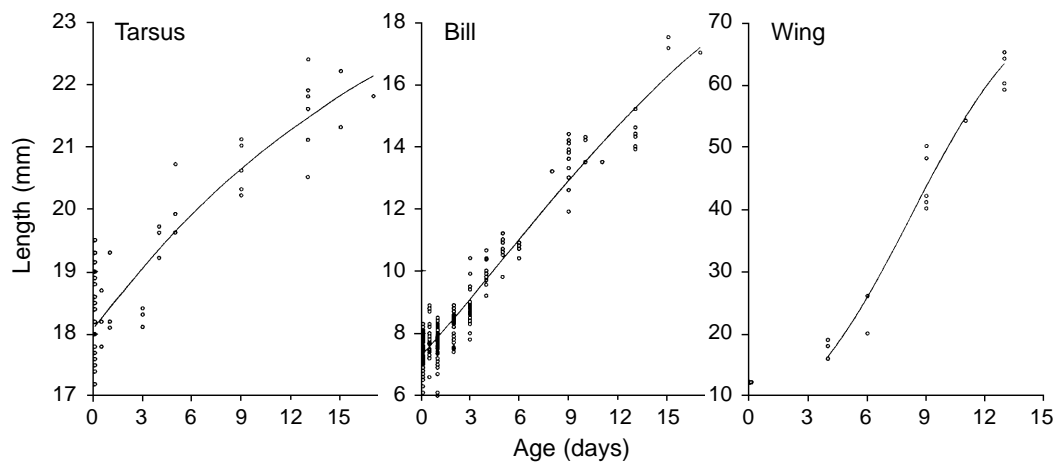


Figure 3. Growth of tarsus, bill and wing length in Little Stints on the Taimyr Peninsula. Observations and fitted logistic curves given for data from all years and locations combined.

realistic estimates of the asymptote. The large variability in tarsus length compared to bill and wing length is probably related to the difficulty in taking this measurement, especially on young chicks.

Like many other precocial waders, Little Stint chicks forage for themselves from the first day onwards. This requires well-developed locomotive and thermoregulatory ability, which is reflected in the large size of the legs at hatching: about 83% of adult size. By contrast, the wing feathers emerged only after about three days. From four days onwards, wing growth was almost linear, and a straight line fitted the data almost as well as the logistic curve ($y = 5.21x - 4.14$; $R^2 = 0.96$). Together

with bill length, wing length is probably the best structure on which to age chicks using measurements. In chicks younger than four days, the early development of the outermost primary feathers is a further helpful ageing clue. In newly hatched chicks, there is usually no sign of these feathers, but after one day the feather germs can be well recognized under the skin. The tips of the feathers in sheaths emerge from under the skin at two to three days of age.

DISCUSSION

The data on Little Stint growth have been collected in a number of years and localities and by several observers, so both observer

Table 3. Growth parameters of Little Stints in Taimyr.

	N	$K_L \pm se$	$A \pm se$	$T \pm se$
Pooled data				
Body mass	163	0.285 ± 0.010	26.65 ± 0.73	7.06 ± 0.28
Bill length	209	0.116 ± 0.010	22.76 ± 2.36	6.20 ± 4.30
Tarsus length	25	0.053 ± 0.249	26.91 ± 8.29	13.96 ± 7.62
Wing length	15	0.254 ± 0.243	87.9 ± 31.5	9.22 ± 3.16
Body mass for separate sites/years				
Knipovich Bay 1990	42	0.309 ± 0.013	26.00 ± 0.90	6.89 ± 0.30
Pronchishchev Lake 1991	19	0.295 ± 0.042	25.35 ± 2.97	6.34 ± 1.22
Pyasina Delta 1990	59	0.239 ± 0.031	29.12 ± 3.69	7.87 ± 1.20

N, the number of chicks contributing observations; K_L , A and T , the parameters of the logistic curve $y(t) = A/(1 + e^{-K_L(t-T)})$, with jackknifed standard errors.^b

effects and site/year variation in growth could have influenced the results. The separate body mass growth curves for the three most extensive data sets were very similar, however, indicating that these factors were of limited influence.

Interspecific comparisons of growth rates in birds have usually been made on the basis of the growth rate parameter K_G of the Gompertz growth equation.^{1,7-8} In Little Stints however, a logistic curve fitted the body mass data better than the Gompertz equation. This applies to several other wader species as well (H. Schekkerman, unpubl. data). Assuming identical asymptotes, the logistic growth rate parameter can be converted to the Gompertz parameter using $K_G = 0.68K_L$,⁸ yielding $K_G = 0.194$ for the Little Stint. Beintema & Visser¹ derived an allometric relationship between asymptotic mass and the Gompertz growth rate parameter K_G in 15 shorebird species: $K_G = 0.390A^{-0.312}$. This equation predicts a K_G of 0.140 for Little Stints, 28% lower and well outside the approximate 95% confidence interval of the observed value. Thus, Little Stints grow at a higher rate than predicted by the allometric relationship. Both the high breeding latitude of Little Stints and the inclusion of relatively slow-growing plovers (Charadriidae) in the allometric equation may contribute to this.¹

Published values of K_G in other small sandpipers are 0.151 for Semipalmated Sandpiper *Calidris pusilla* at 71°N, 0.120 for Baird's Sandpiper *C. bairdii* at 71°N, 0.158 for White-rumped Sandpiper *C. fuscicollis* at 69°N and 0.138 for Dunlin *C. alpina schinzii* at 62°N,¹ whereas data on the Red-necked Stint *C. ruficollis* studied at 66°N yield a K_G of 0.214.⁹ The growth rate of Little Stints (at 73–76°N) was slightly higher than most of these figures, which would be in accordance with an increase of growth rate with latitude. The Red-necked Stint, the only species with K_G as high as that of Little Stints, breeds in montane tundras.^{3,10} The length of the season with temperatures and food availability suitable for growth of wader chicks decreases with both latitude² and altitude, and this is likely to select for rapid growth.

Many shorebirds show a transient delay in body mass growth after hatching,^{1,11-13} although its duration may be very short.⁹ In the Little Stint, a delay in body mass growth was found

but it differed between locations and years. These data suggest that chicks hatch with reserves which can be called upon under some circumstances but that weight loss does not happen inevitably to all chicks. Mass increased most rapidly and from the first day onwards at the Pyasina River mouth in 1990, whereas it decreased during the first and was slower during the second day at Pronchishchev Lake in 1991. During the main hatching period at the Pyasina River in 1990 (17–23 July), the weather was clear with an average temperature of about 10°C, whereas in the main hatching period at Pronchishchev Lake (20–25 July), light rain or snow fell on each day and average temperature was about 5°C. Temperatures were not systematically recorded at Knipovich Bay, but the summer of 1990, when initial growth of Little Stint chicks was slow as well, was generally cold with a warm period only during 23–28 July. Little Stint hatchlings may have stayed in the nest longer under cold conditions, or achieved a smaller net energy gain when they went out to forage due to reduced insect availability,^{11,14} which would both lead to more body reserves being used up during the first days.

The differences in early growth apparently did not lead to differences in size at later ages, in view of the similarity of the growth curves for the three separate data sets. We do not have data to suggest whether slow initial growth was made up by faster growth at later ages or slow-starting chicks suffered higher mortality.

The mass of Little Stint chicks at fledging (23.8 g) and the estimated asymptotic body mass (26.5 g), are close to the average body mass of adult birds during chick-rearing (26.7 g¹⁹). These weights are several grams above the mean mass of 22 g of Little Stints wintering in Africa^{15,16}. This might be explained by the presence of energy stores intended to bridge short-term periods of food shortage, e.g. in the form of cold spells that may occur at any time during the arctic summer. In addition, soon after fledging the juvenile birds start to migrate away from the breeding grounds, and the stored mass may be used as migratory fuel.

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ENDNOTES

a. The growth model developed by Schnute⁵ is a general four-parameter growth model of the form:

$$y(t) = [y_1^b + (y_2^b - y_1^b) \left(\frac{1 - e^{-a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right)]^{1/b}$$

with a and b parameters determining the shape of the curve, and y_1 and y_2 estimates of size at times t_1 in the early and t_2 in the late stage of growth (t_1 and t_2 are chosen by the algorithm on the basis of the data structure). This model was fitted using a procedure written for the statistical computer package Genstat 5.¹⁷ Additionally, three classical three-parameter growth curves (logistic, Gompertz and Von Bertalanffy) were fitted. They are special cases (submodels) of the general model. For instance, restrictions $a > 0$ and $b = -1$ lead to the logistic curve $y(t) = A/(1 + e^{-K(t-T)})$. Although its parameters (asymptote A , growth rate constant K and time at inflexion T) are not the same as those of the Schnute model, they can be obtained in the program output.

b. Chicks were recaptured infrequently and irregularly, and relatively few chicks contribute strongly to the fitted curves. Because the conventional standard errors of the parameter estimates produced by the curve-fitting program assume evenly distributed data, they are inappropriate. Instead, we estimated standard errors using the jackknife technique,¹⁸ by serial exclusion of individual chicks from the data set. This method, however, does not

take full account of the fact that the data consist of unequal groups of observations. Growth may be similar among chicks within the same broods and among broods within a study site/year, causing lack of independence between data points. The jackknifed standard errors should therefore be seen as approximations.

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